Aboveground Biomass of an Invasive Tree Melaleuca (*Melaleuca quinquenervia*) before and after Herbivory by Adventive and Introduced Natural Enemies: A Temporal Case Study in Florida

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Invasive plants can respond to injury from natural enemies by altering the quantity and distribution of biomass among woody materials, foliage, fruits, and seeds. Melaleuca, an Australian tree that has naturalized in south Florida, has been reunited with two natural enemies: a weevil introduced during 1997 and a psyllid introduced during 2002. We hypothesized that herbivory from these and other adventive organisms (lobate-lac scale and a leaf-rust fungus) would alter the distribution and allocation of biomass on melaleuca trees. This hypothesis was tested by temporally assessing changes in aboveground biomass components in conjunction with the presence of natural enemies and their damage to melaleuca trees. Melaleuca trees of different diameters representing the range (1 to 33 cm diam at 1.3 m height) within study sites were harvested during 1996, prior to the introduction of herbivorous insects, and again during 2003 after extensive tree damage had become apparent. Aboveground biomass, partitioned into several components (woody structures, foliage, fruits, and seeds), was quantified both times in Broward, Miami–Dade, and Palm Beach county sites located in south Florida. The two harvests within each site were performed in closely-matched melaleuca stands, and changes in biomass components were compared between years. Total biomass and woody portions decreased in Broward, whereas they increased in Miami–Dade and Palm Beach sites. Reductions in foliage (on all trees) and seed biomass (among seed-bearing trees) were greatest at Broward and least at Miami–Dade County site. Hence, overall seed and foliage production was severely reduced at the Broward site where both the natural enemy incidence and damage were more abundant compared to other sites. We therefore attribute the reduced foliar biomass and reproductive capability of melaleuca trees to infestations of natural enemies. These findings highlight the role that natural enemies can play in the long-term management of invasive tree species.

Nomenclature: Melaleuca, *Melaleuca quinquenervia* (Cav.) S. T. Blake; psyllid, *Boreioglycaspis melaleucae* (Moore); weevil, *Oxyops vitiosa* Pascoe.

Key words: Biological control, *Boreioglycaspis melaleucae*, herbivory, *Oxyops vitiosa*, *Paratachardina* sp., *Puccinia psidii*.

The Australian tree melaleuca is one of the most aggressive exotic plants invading the natural areas of south Florida (Bodle et al. 1994; Hofstetter 1991). Melaleuca occurs in and around freshwater marshes, often associated with the Florida Everglades, but it also thrives in drier areas (Kushlan 1991). It forms monospecific stands by displacing competitively inferior plants in ecologically sensitive communities (Rayamajhi et al. 2006, 2007). Melaleuca trees are erect, up to 25 m tall, with multilayered, thick white or grayish papery bark that insulates the trunk and branches. Terminal inflorescences are indeterminate, 2 to 5 cm long, and arranged in bottlebrush-like spikes. Persistent capsular fruits are arranged in a series of clusters, which can remain attached to the trunks, branches, or twigs for several years (Meskimen 1962). These capsules release seeds when their vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (Hofstetter 1991; Woodall 1982). Massive releases of seeds from reproductively active trees often follow perturbations, resulting in dense melaleuca stands numbering more than 132,000 stems ha^{-1} (Hofstetter 1991; Rayachhetry et al. 2001b). Standing biomass of 129,000 to 263,000 kg ha^{-1} has been reported for melaleuca stands in the United States and Australia (Van et al. 2000). Foliage of a healthy melaleuca tree accounts for > 12% of the total aboveground biomass (Rayachhetry et al. 2001b), and provides the photosynthetic resources that sustain the tree's competitive superiority in its adventive range.

A biological control program targeting melaleuca was initiated in 1986 (Balciunas et al. 1994), with the expectation that introduced herbivores would weaken trees through defoliation, and thereby limit melaleuca's invasive potential. Such expectations were based on the historical evidence of more pronounced insect and disease outbreaks among monospecific forest stands, possibly due to abundance of susceptible hosts (Feeny 1976; Schowalter 2000). Repeated defoliations by the gypsy moth (*Lymantria dispar* L.), for instance, were found to affect the morphology and physiology (e.g., reduced tree growth, increased top dieback, and reduced nonstructural carbohydrate allocation in roots, trunks, and twigs) of poplar [*Populus canadensis* Moench var. *eugenei* (Simon-Louis) Schelle] (Kosola et al. 2001). Consecutive defoliations of perennial trees, e.g., in roots of sugar maple (*Acer saccharum* Marsh) and *Quercus* sp. (Parker and Patton 1975; Wargo et al. 1972) is known to cause declines in total nonstructural carbohydrates. Decreased allocation of carbon to root systems may affect nitrate and ammonium ion uptake and mycorrhizal colonization of root systems, which in turn could cause decreased overall growth and increased plant mortality (Kosola et al. 2001). These effects also expose structural roots to attack by otherwise mildly pathogenic soil microbes as reported for the *Acer saccharum–Armillaria mellea* (Vahl.) Quell. system (Wargo 1972). These records on other woody plants led to the belief that carefully deployed natural enemies could contribute to the melaleuca control efforts in Florida.

The first classical biological control agent, the weevil *Oxyops vitiosa* Pascoe, was released during 1997. Although the adults of the weevil feed on leaves of all ages, its larvae feed on newly developed shoots and cause severe defoliation (Center et al. 2000). The injury resulting from the feeding of this insect did not become widespread until 2001. A second biological

control agent, the psyllid *Boreioglycaspis melaleucae* (Moore), was released during 2002. The nymphs of this insect suck sap from young shoots but also attack older foliage. The localized impact of this insect became apparent by 2003 (personal observation). In addition, an adventive scale insect *Paratachardina* sp. (lobate-lac scale) infests green bark and foliage of melaleuca and other trees and shrubs in several phylogenetically unrelated plant families. This lac scale became prevalent in the south Florida landscape during the spring of 2002 (Pemberton 2003). A sooty mold of unknown identity (indiscriminately covering foliage and green stems) also became abundant, usually in association with heavy infestations of the lac scale (Rayamajhi et al. 2007). In addition, an adventive rust fungus *Puccinia psidii* G. Wint, which infects young foliage of plant species in the family Myrtaceae (Laundon and Waterston 1965; Marlatt and Kimbrough 1979), became an important foliar pathogen of melaleuca during this study period (Rayachhetry et al. 1997).

Early in the development of the melaleuca biological control program, workers assumed that comparisons of aboveground biomass components before and after natural enemy release would elucidate the influences of sublethal herbivory on the invasion potential of melaleuca. Therefore, plant-partitioned biomass was quantified within three melaleuca stands in 1996, prior to the release of herbivorous insects, in an effort to acquire baseline data on plant allometry (Rayachhetry et al. 2001b). Subsequent monitoring of the three stands following the release of natural enemies indicated that herbivore damage varied among stands. The primary objective of this study was to document the temporal changes in patterns of aboveground biomass allocation to various components (particularly foliage and seeds) of melaleuca trees in Florida, as influenced by the damage from adventive and introduced natural enemies.

Materials and Methods

Study Areas. The sites selected for biomass assessment represented typical mature stands that existed in south Florida during 1996 and 2003. These sites became flooded intermittently for several hours to several days following periods of heavy rain but were neither continuously flooded nor flooded every year. Forest floors were generally comprised of poorly-drained organic soils typically classified as Histosols (Brown et al. 1991). South Florida, in general, is characterized by a humid subtropical climate with average monthly temperatures ranging from ca. 19 C in January to 28 C in August to September, and an average rainfall range of ca. 3 cm in January to 27 cm in September (Chen and Gerber 1991).

Site Selection and Tree Sampling. One mixed-age, mature melaleuca stand was selected in each of three counties (Broward, Miami–Dade, and Palm Beach) in Florida during 1996 and again in 2003. A 100 m^2 plot was delineated within each stand for sampling purposes. The plots in Broward and Miami–Dade counties were sampled in 1996 and again in 2003. The Palm Beach County study site had to be relocated to another similarly mature stand with organic soils because the stand sampled in 1996 was destroyed due to herbicide treatment; this relocated site was also sampled in 2003. Edge effects were avoided by placing plots near the center of the stand. Plots were delineated to include the diameter range of the trees typical of the site. All melaleuca trees $\geq$ 1.3 m height within plots were counted, and their diameters were measured at breast height (1.3 m from tree base, hereafter referred to as DBH).

Sample trees representing the DBH range in each plot were randomly selected and then felled at ground level. Total height and DBH of each felled tree was measured. Each tree was considered an experimental unit for statistical purposes. The main trunk and branch components were then separated. The trunk was cut into short, manageable segments with associated bark, weighed fresh, and one of the representative segments was placed in a paper bag and dried to determine the dry to fresh weight ratio. Total branch weight (including branches, twigs, and leaves) was recorded for smaller saplings. A 5 kg random subsample was weighed from larger trees. The branch sample or subsample was then further separated into bare branch, foliage and seed capsule components, and weighed fresh while at the site. These samples plus the trunk-sample segments were oven-dried at 70 C to obtain dry weight, and the oven-dry to fresh weight conversion factor was calculated for each tree. The dry weights of major tree components (trunk, branch, foliage, and seed capsule/seed) were determined for each sample tree by using the conversion factor.

The Broward County site was used to elucidate changes in the amount of aboveground biomass between 1996 and 2003 because it had the most visual differences in tree components, such as foliage and reproductive structures. Prediction equations for aboveground components were developed using the Ln-transformed dry weight (kg) values of the components of individual trees and their corresponding Ln-transformed DBH values as described in Rayachhetry et al. (1998). The resulting allometric equations were used to calculate the biomass components of all trees within the 100 m^2 plots and presented as kg ha^{-1}.

Damage Assessment. Assessments of natural enemy damage were not performed in 1996 because biocontrol insects had not been released and adventive natural enemies were not detected at the time of the study. By 2003, however, damage from the melaleuca weevil and the psyllid, as well as the adventive rust fungus and the scale insect, was widespread in many areas of Broward and Miami–Dade County. To obtain a more quantitative assessment of damage levels, we visually assessed each felled tree for total natural enemy impact, weevil feeding, lobate-lac scale colony incidence, sooty-mold coverage of foliage and green stems, and rust-pustule incidence on foliage. Natural enemy damage, incidence, and impact on each tree were independently assessed as reported in Rayamajhi et al. (2007) by four observers, and the four ratings were averaged. Total tree canopy damage by the insects (weevil, psyllid, and lobate-lac scales) and the rust fungus was rated by four observers as: 0 = no foliage damage or defoliation; 1 = $\leq$ 1% of foliage damage; 2 = 1.1 to 25% foliage damage or defoliation of twigs; 3 = 25.1 to 75% foliage damage or defoliation of twigs; and 4 = 75.1 to 100% foliage damage or defoliation of twigs, and the ratings were averaged.

Individual natural enemy damage, incidence, and impact on each tree were independently assessed as reported in Rayamajhi et al. (2007) by four observers, and the four assessments were averaged. Weevil feeding incidence (percentage of leaves bearing signs of herbivory by weevil larvae and adults), lobate-lac scale incidence (percentage of live bark harboring lac scale colonies on twigs and branches and/or

Table 1. Overall analyses of variance (ANOVA) and analyses of covariance (ANCOVA; LnDBH as covariate) for dependent variables (DBH, height, aboveground tree components) between two measurement years (1996 vs. 2003) among three sites (Broward, Miami–Dade, and Palm Beach) in southeastern Florida.

Dependent variables	Site[a]		Year[a]		Site by Year	
	F	P	F	P	F	P
Plot attributes						
DBH (cm at 1.3 m)[b]	0.84	0.4360	0.00	0.9825	1.97	0.1434
Height (m)[c]	4.17	0.0176	3.11	0.0804	372.56	0.0001
Aboveground biomass (kg tree^{-1})[c]						
Total biomass (all trees)	0.53	0.5876	15.01	0.0002	1308.70	0.0001
Woody materials (all trees)	0.77	0.4615	5.89	0.1670	1457.88	0.0001
Foliage (all trees)	17.50	0.0001	35.27	0.0001	102.85	0.0001
Fruit (all trees)	0.29	0.7503	0.82	0.3656	0.60	0.7294
Fruit (fruit-bearing trees only)	5.71	0.0056	2.17	0.1462	29.14	0.0001
Seed (all trees)	0.53	0.5886	0.52	0.4723	0.81	0.5606
Seed (fruit-bearing trees only)	9.1	0.0004	2.84	0.0976	30.68	0.0001

[a] df (degree of freedom for site, year and site by year were 2, 1, and 6, respectively.
[b] Analysis was based on ANOVA.
[c] Analysis was based on ANCOVA.

percentage of infested leaves), psyllid incidence (percentage of branch tips and leaves with psyllid flocculence and nymphs), rust pustule incidence (percentage of branch tips bearing rust pustules), and sooty mold mycelial felt coverage (percentage of total foliage and stem surfaces with dark-colored mycelial felt coverage) on each of the felled trees in three DBH classes were visually estimated for each tree.

Data Analyses. Statistical analyses were performed using SAS (1999). Normality tests for DBH and tree height (especially for 2003 samples) failed for all sites. Therefore, all of the dependent variables: DBH, height, and biomass components (total, woody materials, foliage, seed capsules, and seeds) were Ln-transformed. DBH of melaleuca trees provided good estimates of aboveground biomass in previous analyses and the amount of the biomass fractions varied by tree diameter (Rayachhetry et al. 1998). In the current study, we tested for height and biomass differences between stands and measurement years (1996 and 2003) with DBH as the covariate. When the P value for the interaction term (Ln[DBH]×YEAR) in the model (Ln[Y] = YEAR Ln[DBH] Ln[DBH]×YEAR); where Y= the biomass component and YEAR = 1996 or 2003) was not significant, the interaction term was dropped from the model when comparing differences among least square means of dependent variables. Categorical overall damage levels (0 to 4) were compared among sites using the chi-square test statistic (Sokal and Rohlf 1981). The percentage of trees bearing the damage levels (0 to 4) was calculated by site and presented in a graphical form to show variation across the diameter range.

Results and Discussion

The interaction between site by year was not different for DBH because samples included trees representing a wide range of diameters (1 to 33 cm) in the studied sites. Overall, the ANCOVA (DBH as covariate) showed significant site by year interactions for tree height and most biomass components, including total biomass, woody materials, and foliage (Table 1). The differences in the amount of fruits and seeds for all (seed-bearing and nonseed-bearing) trees were not significant (Table 1) with the amount of seed varying from 0 to 5 kg per tree. When only seed-bearing trees were included

in the analysis, the site by year interaction was significant for both fruit and seed amounts (Table 1).

Interestingly, the levels of damage inflicted by natural enemies were site-dependent ($\chi^2_{0.05, 8} = 29.35$). Melaleuca trees at the Broward County site exhibited the highest damage ratings (2.8 ± 0.2, i.e., > 25% of the tree canopy damage) whereas those at the Palm Beach County site had the lowest (0.90 ± 0.1, i.e., < 1% of the tree canopy damage). All trees at the Broward and Miami–Dade County sites exhibited natural enemy damage during 2003 (Figure 1). In comparison, about 10% of the trees at the Palm Beach site were undamaged and the remainder were only slightly damaged (Figure 1, Table 2). Weevil, psyllid, lobate-lac scale insect, and rust-fungus injuries were greatest at the Broward County site and lowest at the Palm Beach site (Table 2). During the evaluation period, no evidence of psyllids was observed at the West Palm Beach site. Sooty-mold was present on leaves at all sites. This foliage-blanketing fungus did not cause any physical damage to the trees, but it might have reduced
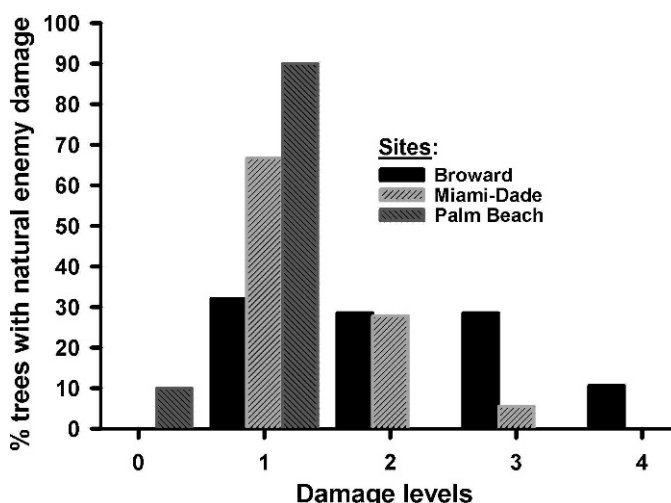

Figure 1. Percentages of sampled trees per site showing levels of natural enemy damage at three sites as assessed during 2003 biomass studies using destructive harvest method. Total damage incurred due to herbivores and pathogen at the scale of 0 to 4 as follows: 0 = no damage; 1 = up to 1%, 2 = 1.1 to 25%, 3 = 25.1 to 75%, and 4 = 75.1 to 100% of the total leaves on a given tree are damaged or defoliated. Chi-squire test showed that the damage level on trees was site specific. Overdamage level in sites was 2.8 (± 0.19), 1.39 (± 0.40) and 0.90 (± 0.09) for Broward, Miami–Dade, and West Palm site, respectively.

Table 2. Natural enemy incidence and impact on melaleuca stand as determined in July 2003 in three County sites of southeastern Florida.

Variables	Broward (n = 28)	Miami–Dade (n = 17)	Palm Beach (n = 20)
		Mean (SE)	
Weevil damage[a]	22.14 (±1.89)[b]a	13.89 (±1.43) b	6.30 (±3.33) c
Psyllid colonies[c]	21.18 (±4.45) a	1.00 (±0.60) b	0.00 (±0.00) b
Rust-fungus pustules[d]	0.18 (±0.70) a	0.00 (±0.00) a	0.10 (±0.07) a
Lobate-lac-scale colonies[e]	26.75 (±3.52) a	2.56 (±1.32) b	2.70 (±1.28) b
Sooty-mold coverage[f]	36.39 (±3.66) a	12.61 (±2.50) b	13.40 (±3.40) b

[a] Percentage of the total leaves showing signs of weevil larvae and adult damage.
[b] Means (SE) among locations within a row with the same letters are not statistically different from each other at P = 0.05 according to Waller–Duncan's multiple range tests.
[c] Percentage of total branch tips and leaves showing psyllid colonies.
[d] Percentage of total tips showing signs and symptoms of rust-fungus damage.
[e] Percentage of total branches and twigs (on live bark), and leaves bearing lac-scale colonies.
[f] Percentage of total live crown covered with mycelial felts of sooty-mold.

photosynthesis and accelerated senescence of the melaleuca foliage (Rayamajhi et al. 2007).

Because the site by year interactions were significant for most of the biomass components, the final ANCOVA was performed by site. The outcomes of the analyses are presented in Table 3.

Broward County Site. About 73% of the trees died at this site between 1996 and 2003 (Table 3). The mean DBH within the stand increased from 1996 to 2003 (Table 3). However, the mean height of trees did not change despite the decreased density. In general, the amount of total biomass,

Table 3. Sample tree attributes, and the analysis of covariance (ANCOVA) on dependable variables representing mean (±SE) of aboveground biomass (kg tree^{-1}) allocation among melaleuca trees in three sites of southeastern Florida as estimated in 1996 and 2003. Values within parentheses in columns 1996 and 2003 represent standard error (SE) of the lsmeans.

Tree attributes	1996	2003	P
Broward County site			
Density (trees ha^{-1})	15,800[a]	4,300	–
DBH (cm)[b]	11.38 (± 1.74)	13.42 (± 1.59)	–
Height (m)[c]	13.01 (± 0.49)	13.06 (± 0.44)	0.4495
Total biomass (kg tree^{-1})[b,d]	64.95 (± 5.72)	56.99 (± 5.17)	0.0047
Woody materials (kg tree^{-1})[b,c]	60.97 (± 5.31)	55.38 (± 4.80)	0.0117
Foliage (kg tree^{-1})[b]	3.05 (± 0.33)	1.23 (± 0.30)	< 0.0001
Fruit (all trees; kg tree^{-1})[b,c]	0.90 (± 0.21)	0.37 (± 0.19)	0.8970
Fruit (fruit-bearing trees; kg tree^{-1})[d,e]	1.82 (± 0.38)	0.76 (± 0.38)	0.0260
Seed (all trees; kg tree^{-1})[b,c]	0.20 (± 0.05)	0.06 (± 0.05)	0.7499
Seed (fruit-bearing trees; kg tree^{-1})[d,e]	0.41 (± 0.09)	0.13 (± 0.09)	0.0071
Miami–Dade County site			
Density (trees ha^{-1})	28,800[a]	11,700	–
DBH (cm)[b]	12.12 (± 1.68)	16.40 (± 2.49)	–
Height (m)[b,c]	9.99 (± 0.36)	9.83 (± 0.43)	0.4838
Total biomass (kg tree^{-1})[b,c]	38.90 (± 5.47)	51.01 (± 6.52)	0.6623
Woody materials (kg tree^{-1})[b,c]	35.85 (± 5.02)	47.57 (± 6.00)	0.9339
Foliage (kg tree^{-1})[b,d]	2.48 (± 0.41)	2.89 (± 0.49)	0.0039
Fruit (all trees; kg tree^{-1})[b,c]	0.45 (± 0.11)	0.40 (± 0.14)	0.3057
Fruit (fruit-bearing trees; kg tree^{-1})[c,e]	1.11 (± 0.29)	1.09 (± 0.33)	0.6468
Seed (all trees; kg tree^{-1})[b,c]	0.08 (± 0.2)	0.07 (± 0.03)	0.3562
Seed (fruit-bearing trees; kg tree^{-1})[c,e]	0.21 (± 0.06)	0.19 (± 0.06)	0.5839
Palm Beach County site			
Density (trees ha^{-1})	10,600[a]	7,900	–
DBH (cm)[b]	13.76 (± 2.09)	11.86 (± 2.47)	–
Height (m)[b,d]	13.62 (± 0.40)	11.84 (± 0.42)	0.0341
Total biomass (kg tree^{-1})[b,d]	57.18 (± 6.75)	72.65 (± 7.08)	0.0331
Woody materials (kg tree^{-1})[b,c]	53.88 (± 6.17)	69.02 (± 6.48)	0.6953
Foliage (kg tree^{-1})[b,d]	2.35 (± 0.24)	1.71 (± 0.25)	0.0184
Fruit (all trees; kg tree^{-1})[b,c]	1.14 (± 0.52)	2.11 (± 0.55)	0.5326
Fruit (fruit-bearing trees; kg tree^{-1})[c,e]	2.28 (± 0.88)	3.31 (± 0.88)	0.1037
Seed (kg tree^{-1})[b,c]	0.21 (± 0.15)	0.59 (± 0.15)	0.8759
Seed (fruit-bearing trees; kg tree^{-1})[d,e]	0.42 (± 0.25)	0.94 (± 0.25)	0.0711

[a] Rayachhetry et al. 2001b.
[b] The least square means presented for the dependent variables were based on total number of trees felled within a given site and harvesting date. N (total number of trees felled) = 23, 24, and 22 in 1996; and 28, 17, and 20 in 2003, respectively in Broward, Miami–Dade and Palm Beach County sites.
[c] Performance of the analyses of covariance (ANCOVA) for dependent variables was accomplished by using the diameter at breast height (DBH) as a covariance. The interaction term (Ln[DBH]×YEAR) was not significant and hence this term was dropped from analysis in final analysis and mean biomass (LN[Biomass] kg tree^{-1}) calculations.
[d] Performance of the analyses of covariance (ANCOVA) for dependent variables was accomplished using the diameter at breast height (DBH) as a covariance. The interaction term (Ln[DBH]×YEAR) was significant and hence this term was used in final analysis and mean biomass (LN[Biomass] kg tree^{-1}) calculations.
[e] The least square means presented for the dependent variables were based on the seed-bearing trees among total number of trees felled in a given sites. N (total number of seed-bearing trees) = 12, 8, and 12 in 1996; and 12, 7, and 12 in 2003, respectively in Broward, Miami–Dade and Palm Beach County sites.

Table 4. Aboveground dry biomass of melaleuca in melaleuca stand of Broward County site in southeastern Florida as measured in 1996 and 2003.

Biomass components	1996	2003
	———kg ha^{-1}———	
Woody materials	323,790	322,310
Foliage	17,500	7,700
Fruit[a]	6,720	1,010
Seed biomass[a]	550	140

[a] Values are based on the seed-bearing trees only.

woody material, and foliage biomass decreased by 12, 10, and 60%, respectively (Table 3). When only reproductive trees (trees bearing fruits and flowers) were included in the analysis, the amount of fruit and seed biomass per tree declined over time (Table 3). The percentage of seed-bearing trees in the sampled population at this site decreased by 9% (52% in 1996 vs. 43% in 2003) (see footnotes, Table 3). Trees at this site exhibited the most overall damage by biological agents (Table 2), which was evidenced by a drastic reduction in foliage, fruit, and seed biomass between 1996 and 2003 (Table 4). Further analysis of the foliage fraction showed a trend in which the foliage biomass decreased disproportionately among smaller trees but remained virtually unchanged among trees with larger DBH (Figure 2). The seed biomass component decreased significantly during the interim but different size classes were not differentially affected (i.e., the slopes of the lines in Figure 2 were equal).

Miami–Dade County Site. Tree density at the Miami–Dade site decreased 69%, although height remained unchanged between 1996 and 2003 (Table 3). Except for the foliage fraction, the biomass of other components remained unchanged between two measurement years (Table 3). The amount of foliage per tree slightly increased (Table 3) though there was a slight decrease among trees of smaller stature (Figure 1). Seed biomass among trees remained unchanged between the two sampling years (Table 3) and increased as DBH increased (Figure 2).

Palm Beach County Site. The amount of foliage per tree decreased, whereas the total biomass increased (Table 3). In contrast, the seed biomass for seed-bearing trees increased by > 100%. Other biomass components did not change (Table 3). Based on the analysis of covariance comparing the foliage fraction between the two dates while adjusting for the effects of tree stature, foliage was reduced somewhat among smaller trees but less so among larger trees (Figure 2). However, the seed biomass among seed-bearing trees showed similar increases across all size classes (Figure 2).

Biological control practitioners rarely quantify natural enemy impact following their field release (Denslow and D'Antonio 2005). The postrelease evaluation can be difficult because impacts can take decades to be realized and replicated herbivore free sites (controls) are challenging to maintain, considering the dispersive nature of natural enemies. Herein, we acquired before and after data from existing stands to demonstrate changes in biomass, which we attributed to natural enemy-mediated damage. In general, negative impacts on melaleuca populations were greatest where natural enemies were well-established. The greater reductions in foliage and seed biomass at the Broward County site compared to the Miami–Dade County sites coincided with higher feeding injury by the
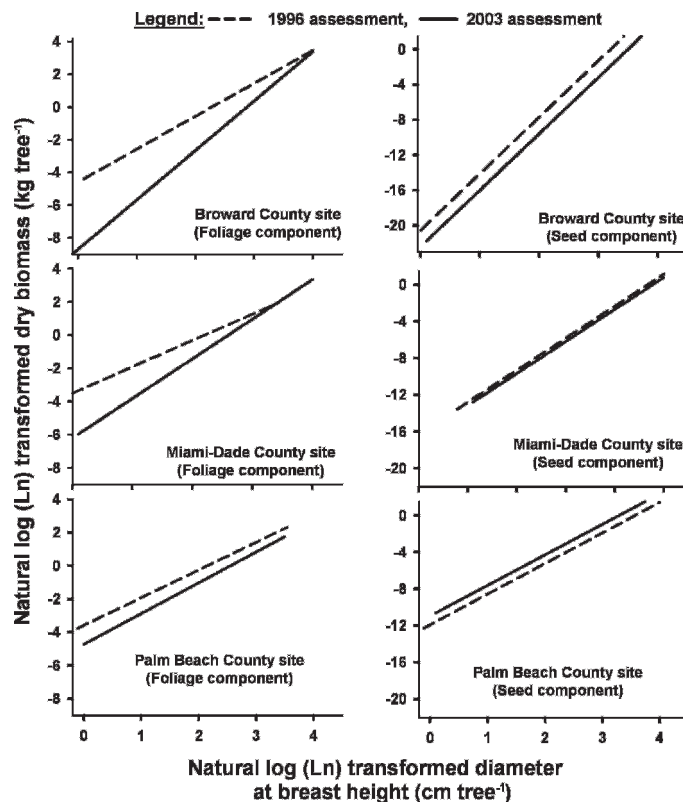

Figure 2. The analysis of Ln–Ln relationship between 1996 and 2003 foliage and seed biomass components of melaleuca trees (using Ln[DBH] as covariant) among three study sites in southeastern Florida. For foliage biomass, LN(Y) = YEAR Ln(DBH) Ln(DBH)×YEAR and for seed biomass, LN(Y) = YEAR Ln(DBH). Because the interaction (Ln[DBH]×YEAR) was not significant for seed biomass, this interaction term was dropped from further analysis and least squared means calculation.

suite of natural enemies. An explanation for the reduction in foliage from 1996 to 2003 at the Palm Beach site remains unclear. One possible explanation is that the trees (in the presence of low density of natural enemies) might have shifted allocation of biomass from foliage to fruit components during our study period. The higher amount of seed at the Palm Beach County site lends support to the above explanation as does the limited abundance or absence of natural enemies during 2003 at that site when the biomass data were acquired.

In most forested systems, the total aboveground biomass of broadleaf trees increases over time despite decreasing stem density (Binkley et al. 2004). Decreasing stem density releases suppressed trees, which undergo enhanced growth. Normally, an increase in diameter growth increases total wood production in melaleuca (Rayachhetry et al. 2001b) and other woody plants (Clough et al. 1997, Nemeth 1973). However, the total estimated aboveground biomass of the melaleuca stand at the Broward site (Table 4), decreased from 348,560 kg ha^{-1} in 1996 to 331,160 kg ha^{-1} in 2003. Attack by natural enemies provided the most plausible explanation for this reduction (Table 3), especially considering the absence of severe weather patterns, fire, or other disturbances during the observation period. Woody biomass, which is largely unaffected by the natural enemies, remained similar from 1996 to 2003 (Table 4). The amount of foliage, fruit, and seed biomass decreased during the same interval by 55, 85, and 74%, respectively (Table 4). Seed reduction might have been the result of several factors, including

reduced transpirational pull due to fewer leaves per tree and the damage to some leaves that remained attached to the twigs, which disrupted the vascular supply of water to the fruits (Rayachhetry et al. 2001a) and forced the fruit to be shed prematurely (Hofstetter 1991).

Among natural enemies, psyllid nymphs caused premature abscission of the leaves of all ages (Morath et al. 2006); and rust pustules induced abscission of immature leaves (Rayachhetry et al. 2001b). This accentuated the effects of the weevils, which defoliated young foliage from stem tips. The combination resulted in trees that appeared progressively more denuded as natural enemy attacks continued unabated.

Sooty-mold, although not directly involved in parasitizing melaleuca trees, obstructs light absorption by covering foliage surfaces and reducing photosynthetic activities. The mold coverage can negatively impact the photosynthesis to respiration rate which can reduce allocation of nonstructural carbohydrates to the root systems (Morath et al. 2006). This phenomenon was observed in an experiment where quantities of nonstructural carbohydrates in the sap of melaleuca leaves were reduced by the melaleuca psyllid (Van, unpublished data). Waring and Pitman (1980) hypothesized that tree vigor is related to the carbohydrate production and reserves, which affect resistance to bark beetle attack. This hypothesis might also be applicable to the melaleuca system in which introduced natural enemies have caused tremendous reductions in carbohydrate production through defoliation and dieback of the tree crown (Pratt et al. 2005).

Overall, the evidence presented in this study indicates that the released and the adventive natural enemies of melaleuca reduced foliage and seed crops in the canopy of mature melaleuca stands. This phenomenon should eventually extend throughout the range of melaleuca in south Florida as populations of existing biological control agents increase and others are established. The existing natural enemies have been credited with substantial reductions in tree density (Rayamajhi et al. 2007). We anticipate that there will be an increase in plant species diversity in areas formerly occupied by melaleuca monocultures.

Acknowledgments

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